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# Importance of water source in controlling leaf leaching losses in a dwarf red mangrove (Rhizophora mangle L.) wetland

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**Importance of water source in controlling leaf leaching losses in a dwarf red mangrove (*Rhizophora mangle* L.) wetland**

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**Abstract**

The southern Everglades mangrove ecotone is characterized by extensive dwarf *Rhizophora mangle* L. shrub forests with a seasonally variable water source (Everglades–NE Florida Bay) and residence times ranging from short to long. We conducted a leaf leaching experiment to understand the influence that water source and its corresponding water quality have on 1) the early decay of *R. mangle* leaves and 2) the early exchange of total organic carbon (TOC) and total phosphorus (TP) between leaves and the water column. Newly senesced leaves collected from lower Taylor River (FL) were incubated in bottles containing water from one of three sources (Everglades, ambient mangrove, and Florida Bay) that spanned a range of salinity from 0‰ to 32‰, [TOC] from 710 to 1400 μM, and [TP] from 0.17 to 0.33 μM. We poisoned half the bottles in order to quantify abiotic processes (i.e., leaching) and assumed that non-poisoned bottles represented both biotic (i.e., microbial) and abiotic processes. We sacrificed bottles after 1,2, 5, 10, and 21 days of incubation and quantified changes in leaf mass and changes in water column [TOC] and [TP]. We saw 10–20% loss of leaf mass after 24 hours—independent of water treatment—that leveled off by Day 21. After 3 weeks, non-poisoned leaves lost more mass that poisoned leaves, and there was only an effect of salinity on mass loss in poisoned incubations—with greatest leaching-associated losses in Everglades freshwater. Normalized concentrations of TOC in the water column increased by more than two orders of magnitude after 21 days with no effect of salinity and no difference between poisoned and non-poisoned treatments. However, normalized [TP] was lower in non-poisoned incubations as a result of immobilization by epiphytic microbes. This immobilization was greatest in Everglades freshwater and reflects the high P demand in this ecosystem. Immobilization of leached P in mangrove water and Florida Bay water was delayed by several days and may indicate an initial microbial limitation by labile C during the dry season.

*Keywords: hydraulic residence time, organic carbon, phosphorus, limiting factor, salinity, Everglades*

## Introduction

Leaf litter fall and decomposition is an important recycling pathway for nutrients and fixed carbon in forested aquatic ecosystems (Fisher & Likens 1973; Brinson 1977; Tam et al. 1990). Although biological processes are important in governing the ultimate fate of leaf litter, evidence from numerous field and lab studies indicates that physical leaching is largely responsible for initial losses of these materials (Brinson 1977; Rice & Tenore 1981; Middleton & McKee 2001 among others). Rates of leaf litter leaching are sensitive to environmental factors such as temperature, sunlight, water availability, and salinity (Nykvist 1959; Nykvist 1961; Parsons et al. 1990; Chale 1993; Steinke et al. 1993). Some researchers have suggested that the biotic contributions in this early stage of decomposition are minimal and most often limited to microbial conditioning of the litter (Nykvist 1959; Cundell et al. 1979; France et al. 1997). Other studies, however, have shown a significant microbial response on fixed carbon and nutrients within the first 24 hours of exposure of leaf material (Lock & Hynes 1976; Benner et al. 1986; Davis et al. 2006).

In tropical mangrove ecosystems, leaf litter leaching rates decline after a few days of immersion in water, yet this process is responsible for substantial losses of elements to the water column and soil (Rice & Tenore 1981; Chale 1993; Steinke et al. 1993; Davis et al. 2003a). On a regional scale, the coupled process of mangrove leaf litterfall and leaching contributes to intra-annual patterns in water quality and materials flux unique to these coastal wetlands (Twilley 1985, Davis et al. 2003b, Maie et al. 2005). This may be particularly important in nutrient-poor, dwarf mangrove wetlands where hydraulic residence times are often high and herbivory rates are very low (Twilley 1995; Feller & Mathis 1997). This combination of ecosystem properties leads to more reliance on internal recycling (i.e., detrital pathways) as a means of controlling nutrient availability and productivity.

The estuarine ecotone of the southern Everglades, FL USA, supports an oligotrophic, P-limited wetland dominated by a dwarf red mangrove (*Rhizophora mangle* L.) forest (Koch and Snedaker 1997). Unlike the Shark River estuary that drains much of the Everglades directly to the Gulf of Mexico, southern Everglades mangrove wetlands are subjected to very low tidal influence (< 5 cm), relatively long hydrologic residence times, and seasonally variable influences of the Everglades and Florida Bay (as described in Chen and Twilley 1999; Davis et al. 2001; Sutula et al. 2003). This leads to different surface water quality signatures in the southern Everglades mangrove ecotone during the dry season (Childers et al. 2005)—when salinity is high and concentrations of dissolved organic carbon (DOC) and total nitrogen (TN) are low—versus the wet season—when salinity is low and [DOC] and [TN] are high (Davis et al. 2003b).

We conducted an experiment to determine how intra-annual patterns of salinity and water source in this dwarf *R. mangle* wetland affect early leaf decomposition and the release and recycling of leached phosphorus and organic carbon. A similar study looking at the effects of salinity on leaching showed that losses of mass and nutrients were greater in *Avicennia* leaves immersed in water with a salinity of 16‰ versus 32‰ (Steinke et al. 1993). Based on these findings, we hypothesized that leaching losses from *R. mangle* leaf litter would be affected by surface water salinity. However, we also expected that source-specific water quality and respective microbial composition would affect leaf-water column exchanges.

Strong phosphorus-limitation across the southern Everglades mangrove ecotone results in low aboveground primary productivity and extremely low litter production (Koch & Snedaker 1997; Coronado-Molina 2000; Ewe et al., 2006). In spite of this, the initial leaching phase of *R.*

*mangle* leaves has been shown to result in a significant release of P and labile organic matter during the first few days of immersion in water (Benner et al. 1985; Davis et al. 2003a). Considering the high degree of P-limitation that exists across the Everglades and into NE Florida Bay (Fourqurean et al. 1992, Amador & Jones 1993, Noe et al. 2001), we expected a rapid microbial response to leached P regardless of the water source and quality experienced by this mangrove wetland.

**Materials and Methods**

In May 1998, we collected newly-senesced, yellow leaves from dwarf red mangrove trees along lower Taylor River, Everglades National Park, FL USA, for use in this experiment. The exact location of the site (FCE LTER site TS/Ph 7b) is longitude -80.649 and latitude 25.214. We conducted the incubations in glass bottles under ambient temperature and sunlight conditions. Following incubation, leaves were removed from the bottles, rinsed with de-ionized water to remove any superficial bacterial layer, and dried to a constant weight at 70°C. The methods for leaf collection and for the leaching experiment are the same used in Davis et al. (2003a).

Since we used fresh leaf material, an accurate means of estimating initial dry weight was needed in order to determine mass loss and to normalize the quantity of total phosphorus (TP) and total organic carbon (TOC) released from each leaf. To accomplish this, we collected an additional batch of newly-senesced leaves (n = 75) from the same site and at the same time to develop a linear regression model that could be used to estimate initial dry mass for each leaf from its initial fresh mass. This model showed that dry mass was consistently 34% of initial fresh mass ($p < 0.0001$; adjusted $r^2 = 0.99$; see Davis et al. 2003a).

Following initial leaf measurements, 100 fresh experimental leaves were individually stored in sterile plastic bags at 4°C for no more than 24 hours. Ninety individual leaves were randomly assigned to treatment combinations according to the experimental design. The three treatments included water treatment (2 levels: with and without poison), water salinity (3 levels: 0‰, 16‰, and 32‰), and collection day (5 levels: 1, 2, 5, 10, and 21 Days). All treatment combinations (water treatment X salinity X collection day) had three replicates.

We added 2 ml of a 1% $NaN_3$ (sodium azide) solution to half of the experimental units as a poison to inhibit biotic respiration. The remaining bottles received 2 ml of de-ionized water. The effect of salinity on the early phase of leaf decomposition was determined by incubating leaves in waters of different salinity. The fixed levels of this treatment were chosen to represent the annual range of salinity and water source common to this dwarf mangrove wetland, as described below. All water was pre-filtered (Whatman GF/F) to reduce variability in large particles (> 0.7 μm) between different waters.

To mimic typical wet season conditions in this dwarf *R. mangle* wetland, we used freshwater collected from a southern Everglades sawgrass (*Cladium jamaicense*) marsh. To get 16‰ water, we collected surface water from within the dwarf *R. mangle* wetland. Water representing the high salinity end member (32‰) was collected from NE Florida Bay. The latter two salinities were intended to reflect surface water conditions found in the dwarf mangrove zone during the dry season or associated with wind/storm events that would bring high salinity water into the dwarf mangrove ecotone from Florida Bay (see Figure 1). We consider the different salinities (0‰, 16‰, and 32‰) of these different sources in our analyses, but also refer to these waters by their respective source (i.e., “Everglades”, “mangrove”, and “Florida Bay”).

Triplicate bottles of each treatment combination were randomly sacrificed after 1, 2, 5, 10, and 21 days of incubation. This sampling protocol allowed for the observation of rapid losses due to leaching (1-2 days) as well as longer term, microbially mediated exchanges (5 days to 3 weeks). During each sampling, leaves were removed from the bottles, water samples were then collected and stored in HDPE bottles at 4°C until analyzed for nutrients. Samples were analyzed for [TP] and [TOC] using methods described in Davis et al. (2003a).

To ensure that changes in water nutrients were solely due to leaf decomposition, control bottles containing only water or water + $NaN_3$ were incubated for the entire 21-day length of the experiment. Nutrient concentrations from the control bottles were compared with initial concentrations to determine changes associated with water column or photochemical processes. Paired t-tests were used to determine significant differences between initial and final concentrations ($p < 0.05$).

We present leaching data for each leaf as occurring under the influence of abiotic processes only (i.e., poisoned) or under the influence of both microbial and abiotic processes (i.e., non-poisoned). We used ANOVA to determine the effect of water treatment, salinity, and collection day on the percentage of dry mass remaining (%DMR) in each leaf and on [TOC] and [TP] of water in each bottle. These concentrations were normalized to the initial dry mass of each leaf. For all analyses, Tukey-Kramer post-hoc tests were used to determine differences between treatment means of significant ANOVAs ($p<0.05$).

**Results**

Rapid losses of mass occurred in each water treatment level, as 10–20% of the initial dry mass of leaves was lost after 24 hours (Table 1). After Day 1, changes in percent dry mass remaining (%DMR) from one sampling to the next were more gradual. Overall, mean %DMR was significantly higher in poisoned bottles (Table 1). For the most part, early differences in %DMR between poisoned and non-poisoned incubations were negligible. However, after five days of incubation, the differences in %DMR between bottles with and without $NaN_3$ became more noticeable, especially at lower salinities (Table 1).

The contribution of microbial processes to the loss of mass from individual leaves appeared to increase over time. However, we observed a difference in mean %DMR between poisoned and non-poisoned incubations only in 0‰ and 16‰ water, with non-poisoned bottles showing greater losses of mass (Table 2). Finally, we detected an effect of salinity on mean %DMR only in leaves immersed in water containing the poison (Table 1). Percent dry mass remaining due to leaching (i.e., abiotic processes only) was significantly higher in 16‰ water than in freshwater, and %DMR in leaves leached in 32‰ water could not be statistically differentiated from either (Table 1).

The use of water from different sources resulted in differing initial concentrations of TOC and TP for the different salinity levels, but the differences did not exceed a factor of two (Table 3). These differences did not seem to affect the outcome of the experiment for either TOC or TP exchange, as concentrations of each constituent increased by more than an order of magnitude after 21 days of leaf decay. Control bottles (i.e., those without leaves) showed no significant changes in [TOC] or [TP] from day 0 to day 21, either with or without poison.

Water nutrient content at each sampling time was normalized to the initial dry mass of the leaf in each bottle (moles gdw $leaf^{-1}$). There was no statistical difference in [TOC] between poisoned and non-poisoned incubations. However, normalized concentrations of TOC after 21 days were noticeably lower in non-poisoned bottles (mean = 181.2 mmoles TOC $gdw^{-1}$) compared to poisoned bottles (mean = 224.1 mmoles TOC $gdw^{-1}$). We observed a significant time effect on normalized values for [TOC] regardless of the addition of poison ($p < 0.0001$;

Figure 2). The trend for TOC was a rapid rate of release (moles gdw leaf$^{-1}$ day$^{-1}$) to the water column within the first two days followed by more gradual releases over the latter half of the study. The cumulative effect was significantly higher normalized [TOC] in bottles after 21 days (Figure 2). Normalized TOC concentrations after 1, 2, 5, and 10 days could not be differentiated from one another. We saw no effect of salinity on the release of TOC from dwarf *R. mangle* leaves in either poisoned or non-poisoned incubations.

Overall, total phosphorus concentrations in poisoned incubations were not different from [TP] in non-poisoned incubations (Figure 3). There was a significant water source effect on [TP] in non-poisoned bottles ($p < 0.0001$). Mean TP concentrations were highest in 16‰, followed by 32‰, and were lowest in 0‰ despite relatively high initial [TP] concentrations in this treatment (Figure 4; Table 3). This water source effect was especially noticeable during the Day 5 and Day 10 samplings, when normalized TP concentrations were highest in 16‰ and lowest in 0‰. After Day 10, the TP content of these bottles decreased by nearly half—from a mean of 7.1 to 2.9 µmoles TP gdw$^{-1}$ (Figure 3).

In the non-poisoned incubations, we saw no significant change in TP concentrations through time in 0‰ water (Figure 3). In the 16‰ and 32‰ salinity levels, [TP] was highest after 5 days and then leveled off or declined by Day 21.

We saw no evidence of a water source effect in bottles containing poison. In addition, total phosphorus in poisoned incubations followed an increasing trend over three weeks with values leveling off at a mean of 5.1 µmoles TP gdw$^{-1}$ after 10 days (Figure 3).

## Discussion

Our findings reflect those shown in numerous other studies regarding the importance of leaching in the early loss of materials from leaf litter (Brinson 1977; Rice & Tenore 1981;

Ibrahima et al. 1995; among others). By isolating the contribution of abiotic processes in the poisoned incubations, our data also reveal the role that biological processes play during this stage of *R. mangle* leaf decay. This study also sheds light on the importance of water source in affecting the early decay of leaf litter in this seasonally dynamic oligohaline ecotone of Everglades National Park.

*Leaching vs. Microbial Contributions to Mass Loss*

Leaching (i.e. abiotic processes) resulted in mean losses of 18% of leaf mass after 2 days and up to 30% after 3 weeks. These losses were comparable to other studies on temperate deciduous and tropical mangrove leaf litter (Tam et al. 1990; Steinke et al. 1993; Chale 1993; Ibrahima et al. 1995; France et al. 1997). Some of those studies showed that leaching-associated mass loss, although rapid at first, tended to level off within a few weeks (Steinke et al. 1993; Ibrahima et al. 1995; France et al. 1997). However, others have suggested that leaching may be an important part of the decomposition of mangrove leaf litter for up to a month (Cundell et al. 1979; Tam et al. 1990).

We found that microbial contributions to mass loss were minimal at first, but gradually increased over the three-week study period. After 21 days, biotic processes (i.e., non-poisoned %DMR minus poisoned %DMR) accounted for approximately 4–14 % of dry mass loss from *R. mangle* leaves. These microbially mediated losses were greatest in Everglades freshwater and lowest in Florida Bay water (salinity = 32‰). We believe that this may have been a result of the differences in the quantity and quality of dissolved organic material and corresponding microbial biomass of the different sources of water used in the experiment. Everglades water that had the highest initial [TOC] may have also had relatively high bacterial densities that may have influenced decay rates and leaf-water column exchanges. FCE-LTER data on bacterial abundance across this region of the southern Everglades and into Florida Bay suggest that 1) bacterial abundances are highest in the mangrove ecotone and during wet season months when runoff from the Everglades is high, and 2) bacterial abundance is lowest in Eastern Florida Bay relative to these Everglades marsh and mangrove sites as well as central and western Florida Bay, where seagrass productivity is considerably higher (Fourqurean, et al. 1992; J. Boyer, unpublished data).

We did not attempt to quantify the difference in bacterial densities among our source waters. However, a study conducted on red mangrove leaves immersed only in eastern Florida Bay (salinity = 33.5‰) found that bacterial colonization of the leaves was not detected until after 28 days of submergence (Cundell et al. 1979). The slow colonization was likely attributed to the relatively low TOC content and subsequently low initial bacterial biomass of this water.

*Leaching vs. Microbial Contributions to TOC and TP Dynamics*

We found that leaching was considerably more important than microbial processes (such as bacterial mineralization) in governing TOC exchange over three weeks of leaf immersion. At the conclusion of our experiment, we found that water column [TOC] increased by as much as two orders of magnitude in poisoned and non-poisoned incubations. However, significant microbial activity was apparent, as leaf surfaces in the non-poisoned bottles had a well-developed, mucous layer after 10 days. Non-poisoned bottles also showed indications of anaerobic activity, as we detected a strong sulfidic odor in both 16‰ and 32‰ bottles after 10 days. Lastly, there was also a noticeable difference in 21-day [TOC] means between poisoned bottles and non-poisoned bottles, indicating that a sizable portion of leached TOC had been respired (Figure 2).

From a mass balance standpoint, carbon accounted for a small percent of leaf mass losses after one day (< 5%) across all treatments. This was the period of time in which the greatest single loss of mass occurred. Considering that the contribution of carbon to mass loss was delayed and the mass loss attributed to phosphorus was trivial, some other elements must have accounted for the large initial losses. Evidence from other studies has suggested that ions such as K, Ca, Mg, and Mn contribute to the large, initial losses of mass from leaves (Steinke et al. 1983; Tam et al. 1990; Chale 1993; Steinke et al. 1993). At the conclusion of our experiment, carbon loss accounted for as much as 30% of the mass loss associated with leaching after three weeks of decomposition. By comparison, Ibrahima et al. (1995) found that carbon accounted for 50-80% of mass loss from deciduous leaves after 10 days of decomposition.

Although phosphorus was a minor component in terms of mass loss, the process of leaching appears to be a significant source of phosphorus to this P-limited ecosystem. In all incubations, normalized [TP] increased more than three-fold after just five days. When microbial processes were absent, leachable TP seemed to be exhausted after 10 days, regardless of salinity, indicating that leachable P was depleted rather quickly. Evidence of this rapid depletion of leachable P exists for other tree and wetland macrophyte species as well (Meyer 1980; Twilley et al. 1986; Rubio & Childers 2006). This release of TP during the first few days of leaf immersion is likely critical in sustaining levels of primary and secondary productivity in oligotrophic mangrove wetlands such as those found along lower Taylor River.

We observed water source/salinity effects in bottles with an active microbial community that were likely the result of P-limitation and pre-existing microbial densities in the source waters. At one extreme, TP release in non-poisoned mangrove and Florida Bay water peaked at about 5 days, then leveled off or declined to a mean of about 3.4 µmoles $gdw^{-1}$. Whereas mean

[TP] in non-poisoned Everglades water showed no significant change over the duration of the experiment, fluctuating between daily means of 1.1 and 2.3 µmoles gdw$^{-1}$. When this pattern was compared with poisoned bottles containing the same source water, it suggested a rapid response (< 24 hours) to leached P and sustained interception of leached P by epiphytic microbes contained in Everglades freshwater. Meyer (1980) observed a similarly rapid uptake of leached P after 48 hours in Bear Brook (NH), also a likely result of microbial immobilization.

In our study, there was a similar microbial response to leached P in mangrove and Florida Bay water, but this response took as long as 5–10 days to develop. This could mean that the low organic content of these source waters and correspondingly low microbial densities were limited more by labile carbon at the outset of the experiment. As leached TOC met these requirements, TP then became limiting, resulting in the significant drop in normalized TP in mangrove and Florida Bay water. A similar leaf incubation or *in situ* chamber study using glucose additions would help address the question of C versus P limitation at different stages of decay and during different seasons (wet vs. dry) of the year in this system.

Based on the water source effects we observed in this study, the early decomposition of dwarf *R. mangle* likely leaves varies seasonally. This seasonal variability is due, in part, to seasonal driven factors such as light intensity and temperature. However, given the variability in residence time and the different sources of water to the dwarf mangrove zone of the southern Everglades, our data suggest that seasonal differences in water quality (i.e. salinity, DOM quantity and quality, bacterial densities, etc.) may account for intra-annual variations in decay rates. Nutrient release rates from these leaves might also vary seasonally, affecting the amount of leached P and labile C available to benthic and water column organisms. Given the variations in hydraulic residence time in this region, this could lead to variations in surface water quality (i.e., [P] and [OC]) as well as the quality of standing detritus pools, both of which would directly affect water column and benthic metabolism within these oligotrophic wetlands.

## Conclusions

Our findings suggest that leaching losses were not affected by salinity alone. However, site-specific water quality characteristics were important in determining P dynamics associated with the early decay of dwarf *R. mangle* leaves. Further, these findings shed light on other ecosystem properties—such as the availability of labile organic carbon and hydrologic residence time—that may govern the availability and cycling of phosphorus in the surface water of this oligotrophic P-limited wetland.

From this, we hypothesize that labile organic carbon may be depleted in the water column of this dwarf mangrove wetland when residence times are long, resulting in low microbial densities. During these periods, we believe that P addition to the water column via the leaching of leaf litter may not elicit a significant, immediate microbial response due to a limitation by C. As a result, water column [P] may increase well above normal levels in periods of low flushing. When sufficient amounts of labile C are added to the system, via leaf litter leaching or from Everglades runoff, the water column would then shift back to a P-limited environment, resulting in low water column [P]. Evidence of this phenomenon (i.e., high [P] in periods of high salinity and long residence time and low [P] in periods of low salinity and shorter residence time) exists in long-term surface water monitoring data from this dwarf mangrove system (Davis et al. 2001a; Davis et al. 2001b; Childers et al., 2005). However, continued monitoring and long-term research projects addressing these ideas are needed.

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**Sources of Unpublished Materials**

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Table 1: Treatment means (± stdev) for % dry mass remaining. Different letters represent significant differences between treatment means (ANOVA, Tukey-Kramer post-hoc test; p<0.05).

| **Poisoned [a]** | | | | | **Non-Poisoned [b]** | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 0.792 ± 0.065 | | | | | 0.740 ± 0.102 | | | | |
| **0‰[a]** | | **16‰[b]** | | **32‰[ab]** | **0‰[a]** | | **16‰[a]** | | **32‰[a]** |
| 0.767 ± 0.043 | | 0.814 ± 0.060 | | 0.791±0.082 | 0.708 ± 0.107 | | 0.749 ± 0.063 | | 0.763 ± 0.124 |
| **day 1[a]** | **day 2[ab]** | **day 5[bc]** | **day 10[cd]** | **day 21[d]** | **day 1[a]** | **day 2[ab]** | **day 5[b]** | **day 10[c]** | **day 21[d]** |
| 0.838 ± 0.052 | 0.829 ± 0.044 | 0.793 ± 0.055 | 0.767 ± 0.059 | 0.727 ± 0.053 | 0.827 ± 0.031 | 0.796 ± 0.076 | 0.761 ± 0.066 | 0.692 ± 0.083 | 0.625 ± 0.095 |

Table 2: Treatment means (± stdev) at each salinity level showing the effect of poison on % dry mass remaining in *R. mangle* leaves. Different letters represent significant differences between treatment means (ANOVA, Tukey-Kramer post hoc analyses; $p < 0.05$).

| **Salinity** | **Poisoned** | **Non-poisoned** |
|---|---|---|
| 0‰ | $0.767^{a} \pm 0.043$ | $0.708^{b} \pm 0.107$ |
| 16‰ | $0.814^{a} \pm 0.060$ | $0.749^{b} \pm 0.063$ |
| 32‰ | $0.791^{a} \pm 0.082$ | $0.763^{a} \pm 0.124$ |

Table 3: Mean (± stdev) initial [TOC] and [TP] in different source waters used for mangrove leaf leaching experiment.

| Salinity | [TOC] (μM) | [TP] (μM) |
|---|---|---|
| 0 ‰ | 1400 ± 19 | 0.23 ± 0.04 |
| 16‰ | 897 ± 23 | 0.33 ± 0.07 |
| 32‰ | 710 ± 14 | 0.17 ± 0.06 |

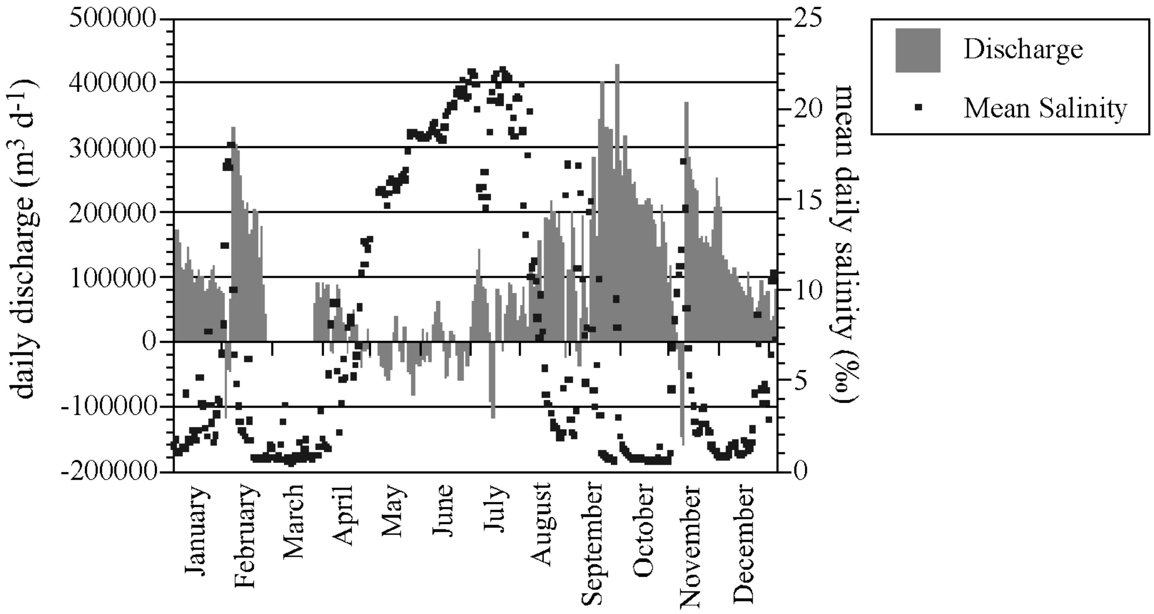
**List of Figures**

Figure 1: 1998 hydrograph of lower Taylor River, Everglades National Park (FL), showing daily discharge and mean daily salinity. Data are from USGS gage # 251127080382100.

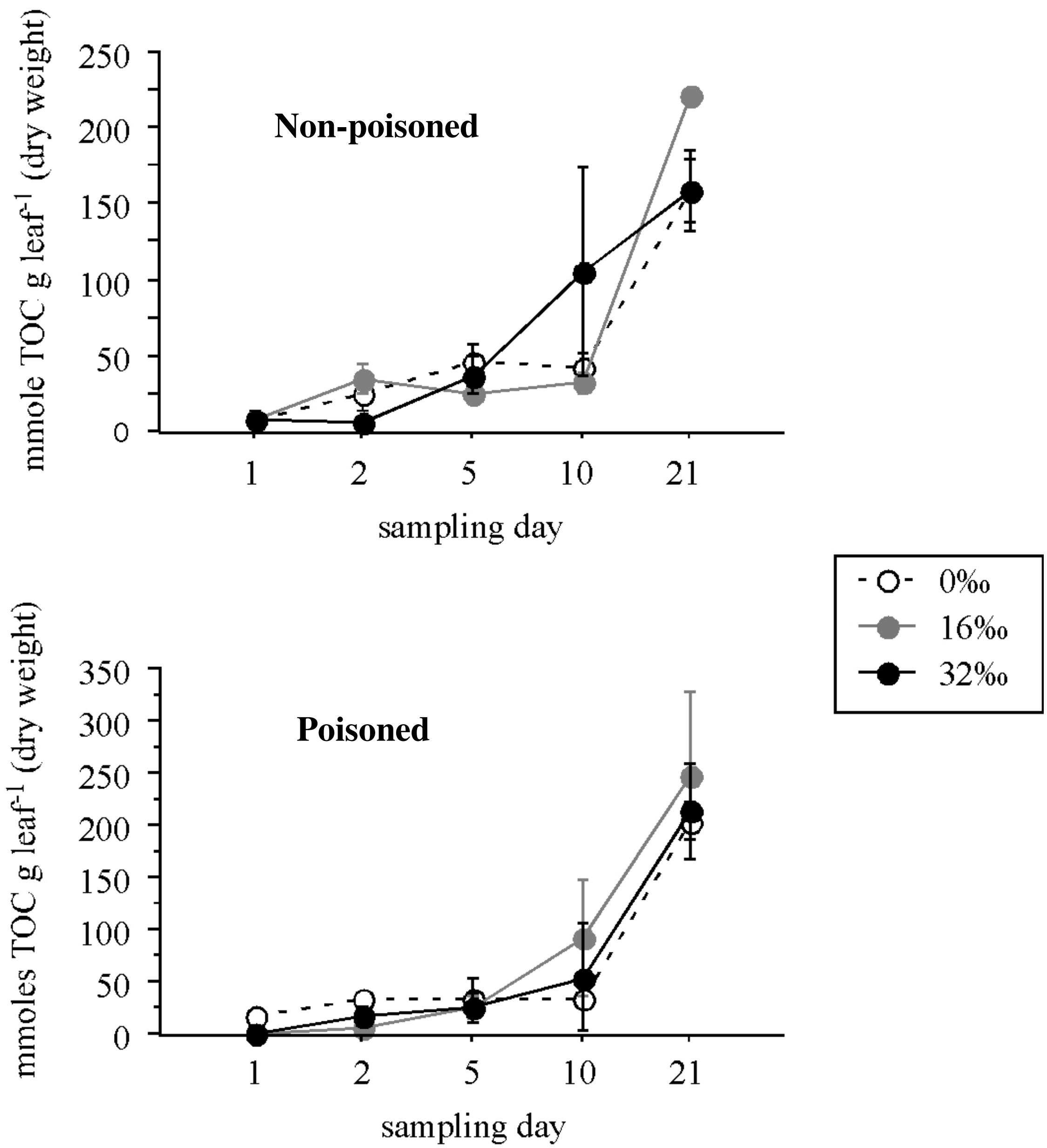
Figure 2: Time-series plots of normalized [TOC] by salinity in poisoned (bottom) and non-poisoned (top) incubations.

Figure 3: Time-series plots of normalized [TP] by salinity in poisoned (bottom) and non-poisoned (top) incubations. Asterisks indicate sampling days where we observed a significant salinity/water source effect.

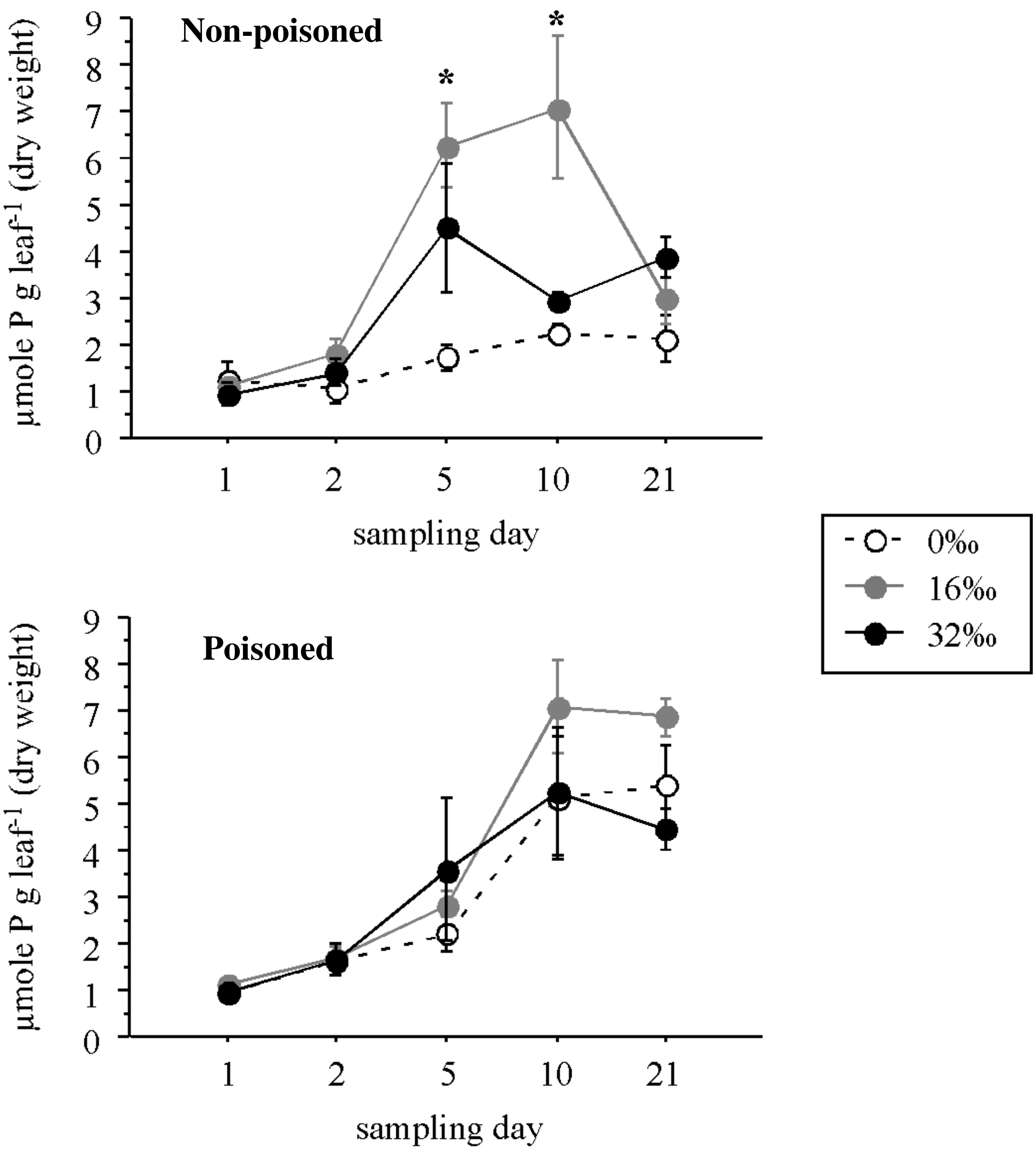
Figure 4: Box plots of normalized [TP] distributions in each salinity/water source category over the duration of the non-poisoned incubations. Different letters indicate significant differences.

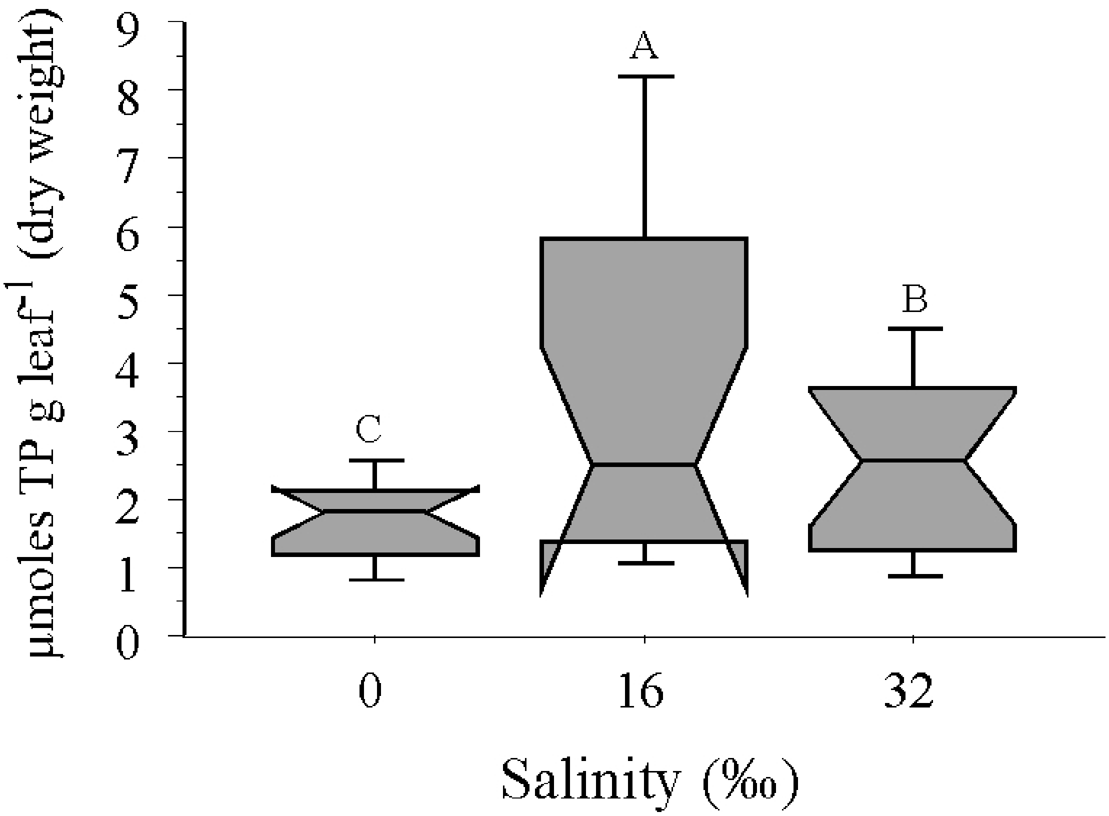


500000
400000
300000
200000
100000
0
-100000
-200000
daily discharge (m3 d-1)
25
20
15
10
5
0
mean daily salinity (‰)
January
February
March
April
May
June
July
August
September
October
November
December
Discharge
Mean Salinity



mmole TOC g leaf-1 (dry weight)
250
200
150
100
50
0
Non-poisoned
1
2
5
10
21
sampling day
0‰
16‰
32‰
mmoles TOC g leaf-1 (dry weight)
350
300
250
200
150
100
50
0
Poisoned
1
2
5
10
21
sampling day


Non-poisoned
Poisoned
μmole P g leaf-1 (dry weight)
0
1
2
3
4
5
6
7
8
9
*
*
1
2
5
10
21
sampling day
0‰
16‰
32‰

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